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Prey and nesting preferences of the alien wasp *Isodontia mexicana* (Hymenoptera, Sphecidae) in southern Germany

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Abstract

Isodontia mexicana (Sphecidae) is a neozoic wasp in Europe. Since its first recording in France in the 1960s, it has spread throughout Europe and is now considered established. It preys on grasshoppers for its larvae but so far, there is little empirical evidence on the composition of prey species and the wasp's preference for nest tube diameters from Europe. For further insights into prey and nesting preferences, we placed layer nests with 4 different cavity diameters in contrasting habitats in Southwest Germany. The wasp's prey consisted of two grasshopper species, *Oecanthus pellucens* and *Meconema meridionale*. For *O. pellucens*, 80% of the prey found were female, for *M. meridionale* 52% and the mean body length of *M. meridionale* was 11.92 mm (SD = 0.95) and that of *O. pellucens* was 12.31 mm (SD = 1.02). The preferred cavity diameter for nests was 11 mm, with preference given to deeper cavities within the offered layer nest. The flexibility in prey species may reduce the threat for individual prey species populations, but may allow further spread of the Sphecid wasp. However, the preference for relatively large diameters reduces the expected competition risk with native bees below previous expectations.

Keywords

Bee house, bees, ecological niche, insect, invasive species, nesting competition

Introduction

Isodontia mexicana is a digger wasp of the Sphecidae-family native to North America. Between 1940 and 1960, *I. mexicana* was probably introduced to Europe by US supply troops via France (Bosch et al. 2018). Since then, it has been spreading continuously; both naturally and via unintentional transport of its brood by humans, e.g. in reeds and bamboo sticks for garden use (Hellrigl 2004; Bosch et al. 2018). Since 1962, it has been found in at least 16 European countries (Bosch et al. 2018). The first record in Germany was in 1997 in Tübingen, Baden-Württemberg (Westrich 1998). The most northern reports come from Berlin (Saure et al. 2019), and England (Notton 2016). The adults of *I. mexicana* occur in many habitat types; they have been found in open landscapes, residential areas, private gardens and city parks (Bosch et al. 2018). Their large, black shape with the metallic-blue wings makes them easy to identify in the field (Fig. 1A, B).

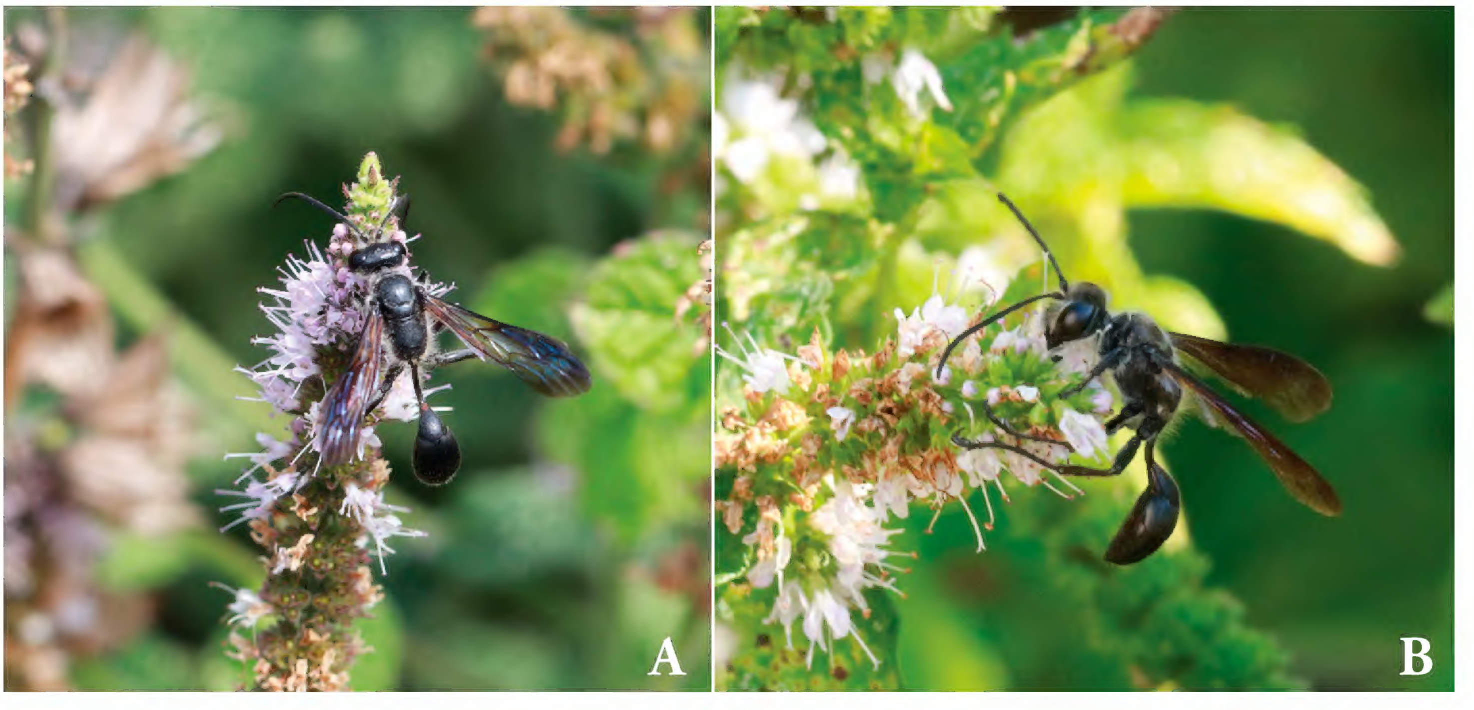

Figure 1. A, B a portrait of the Sphecid wasp *Isodontia mexicana* with its shiny blue wings.

Nesting activity and competition with bees

Isodontia mexicana builds its nests in small above ground cavities, including reed and bamboo tubes commonly used in insect houses or even old breeding tubes of *Xylocopa violacea* (Rennwald 2005; Bosch et al. 2018). Therefore, it is a potential competitor for nesting sites with native cavity-nesting bees. Multiple brood cells are provisioned with grasshoppers and separated by walls made from grass stalks, a unique material for cavity nesting Hymenoptera in Europe (Hellrigl 2004) (Fig. 2). The diameter of the nest tube defines which insect species may nest in the cavity, the preference of *I. mexicana* varies greatly in the literature. American studies indicate that highest occupancies occurred at 6.4 mm (Medler 1965) to 7 mm (O'Neill and O'Neill 2003), while in European literature diameters of 8 to 9, rarely also 10 mm have been described (Schirmel et al. 2020).

Figure 2. Layer nest board with fresh *I. mexicana* nests in 11 and 9 mm drillings. Brood cells are (sometimes loosely) separated and closed by grass sticks and filled with paralysed grasshoppers as food for their developing larvae.

Based on the size of the cocoon of the mature larva of *I. mexicana*, Medler assumes that 4.8 mm could be the smallest possible radius of the nest tube (Medler 1965). Bees, native to Germany and likely northern central Europe, generally use diameters

of 2 to 8 mm (Westrich 2019). However, which and whether there is competition for nesting space can only be assessed when more precise information on preferred diameters of *I. mexicana* is available. The sex ratio of *I. mexicana* offspring is roughly balanced, although there are nests with mixed-sex larvae or of only one sex. However, when both sexes are present in a breeding tube, the female larvae always lie in the rear, first created brood cells and hatch slightly later than the males (Medler 1965; O'Neill and O'Neill 2009). Mating usually occurs immediately after hatching.

Food and nesting sites

Like all digger wasps, *Isodontia mexicana* is specialised in one prey order, it feeds on grasshoppers (Orthoptera) of the suborder Ensifera as larval food (Timm et al. 2024). The hunting behaviour for Ensifera has not been described in the literature so far, but the variety of prey items inhabiting treetops and grasslands indicate that *I. mexicana* hunts for prey in different habitats (Medler 1965). The traits determining prey selection and subsequent placement in nests is not described. However, *I. mexicana* builds several nests at the same time and potentially decides to place larger prey items into the more spacious nest cavities. Since *I. mexicana* deliberately provides female offspring with more food than male offspring (O'Neill and O'Neill 2003) and the number of eggs in a nest correlates more with prey weight than with the number of prey individuals (Medler 1965), it is reasonable to assume that the female is aware of the physical parameters of the prey. This raises the question of a preference for cavity diameters and whether the diameter of the nest tube can be associated with the size of the prey.

Ensifera are mostly nocturnal, but *I. mexicana* prey collection takes place during the day (Bosch et al. 2018). For example, the cricket *Oecanthus pellucens* only becomes active at dusk and reaches its activity peak at complete darkness. During the day, the crickets rest in or on plants, e.g. in older, rolled-up leaves, where they are excellently camouflaged by their heterogeneous brown body colour (Horstkotte et al. 1991; Fischer et al. 2016). The Ensifera species *Meconema thalassinum* and *M. meridionale* rest during the day on the underside of leaves in bushes or trees (Fischer et al. 2016). However, whether activity mismatch affects prey collection success is unknown but it indicates that *I. mexicana* is using visual or olfactory cues to locate its prey. In contrast to its larva, adult *I. mexicana* feed on nectar of flowers. Seasonally, they show a preference for Apiaceae and Asteraceae, mostly visiting yellow and white flowers (Pernat et al. 2022).

None of the prey species documented from North America occur in Europe. Documented are in total nine species of Ensifera in Europe, Italy (seven), Germany (five) and Switzerland (one), see Table 1.

In its native range, the prey spectrum includes several Ensifera species, especially *Conocephalus* sp. (Tettigoniidae) and *Oecanthus* sp. (Gryllidae) (Medler 1965; O'Neill and O'Neill 2003). The species *Oecanthus pellucens*, documented in *I. mexicana* nests in Germany, is most similar to the original prey (Scaramozzino and Currado 1988). In southern Germany, Schirmel et al. (2020) showed that with decreasing prey size, the number of individuals in a brood cell increased. Of these 95% were

Table 1. An overview to documented prey species of *Isodontia mexicana*.

Prey species	Country	Reference
Conocephalus discolor	Italy	(Scaramozzino and Currado 1988)
Leptophyes punctatissima	Germany	(Schirmel et al. 2020)
Meconema meridionale	Italy	(Scaramozzino and Currado 1988)
	Germany	(Schirmel et al. 2020)
	Switzerland	
Meconema thalassinum	Italy	(Scaramozzino and Currado 1988)
	Germany	(Schirmel et al. 2020)
Oecanthus pellucens	Italy	(Scaramozzino and Currado 1988)
Phaneroptera nana / falcata	Italy	(Scaramozzino and Currado 1988)
	Germany	(Schirmel et al. 2020)
Pholidoptera griseoaptera	Germany	(Schirmel et al. 2020)
Pholidoptera spec.	Italy	(Scaramozzino and Currado 1988)
Ruspolia nitidula	Italy	(Scaramozzino and Currado 1988)

Meconema thalassinum and *M. meridionale* in the 4^{th} or 5^{th} larval instar, but *Oecanthus pellucens* was not found and equal number of male and female were collected (Schirmel et al. 2020). To identify if *I. mexicana* adapts is prey choice in terms of species and sex on the availability or other cues its brood cell provisioning needs to be studied in different habitats with distinct Orthopteran species.

Specifically, we addressed the following questions. What is the preferred cavity diameter of *Isodontia mexicana*? Are cavity diameters different between habitats with different prey species and is prey size correlated with cavity diameter?

Methods

To sample nests of *Isodontia mexicana*, trap nests were placed in the two different habitats south-west Germany, specifically in Freiburg im Breisgau and Ihringen with expected different abundances of potential prey species. The layer nests were inspected twice a week for nests of *I. mexicana* and brood cell content analysed.

Structure of the layer (trap) nests

Trap nests were made by carving cavities of 13.5 cm length and diameters of 5, 7, 9 and 11 mm into 15 × 15 × 1.8 cm medium-density fibreboards (layer boards). Six boards, the upper one covered by a board without cavities, were stacked and strapped together to form one layer (trap) nest. Each diameter was carved twice per panel, giving 12 carvings per diameter per layer nest. Layer nests were installed at sun exposed locations with cavity openings oriented towards south to south-east. The egg development time is not known, but larva of *I. mexicana* need at minimum 4 to 6 days from hatching to feed on its prey and pupate. To collect all prey items, nests were inspected every 4 to 5 days. On each inspection all cavities were checked, number of brood cells, wasp eggs

or larvae recorded and prey items sampled per brood cell. Species were identified using the Deutscher Jugendbund für Naturschutz (DJN) Observation key (Horstkotte et al. 1991), additionally sex, body length and weight of each prey individual were determined. We defined brood cells as nests if the cells created contained an egg and were closed, as we also found closed cells without eggs, which we assumed to be mock nests.

Locations of the layer nests

To identify habitats of *I. mexicana* with distinct prey communities, distribution areas of the known prey species *Meconema* sp. and *Oecanthus pellucens* in the vicinity of Freiburg were assessed. Information from the website of the German Society for Orthopterology (www.dgfo-articulata.de), the Swiss platform for grasshopper science (www.Orthoptera.ch) and the social network for nature observation (www.iNaturalist.org) were used. *Meconema* sp. was found in Freiburg and also Ihringen. *Oecanthus pellucens* was only present in the warm arid vineyard areas around Ihringen at the Kaiserstuhl, whereas, *M. meridionale* and *M. thalassinum* were more present in gardens and proximity to humid forests around eastern Freiburg. In each of the two habitats, six layer nests were installed (Fig. 3).

To establish layer nest sites private garden owners and the administrations of municipal gardens and parks were contacted. Sites were at least 300 m apart to achieve a high degree of coverage of the studied habitats. The exact flight radius of *I. mexicana* is not known, but flight distances between individual flowers of 140 m have been observed (Bosch et al. 2018). Therefore, a minimum distance of 300 m seems plausible to prevent the same *I. mexicana* female from occupying layer nests at several sites. To increase the colonisation rate at each habitat type trap nests were preferably placed next to preexisting

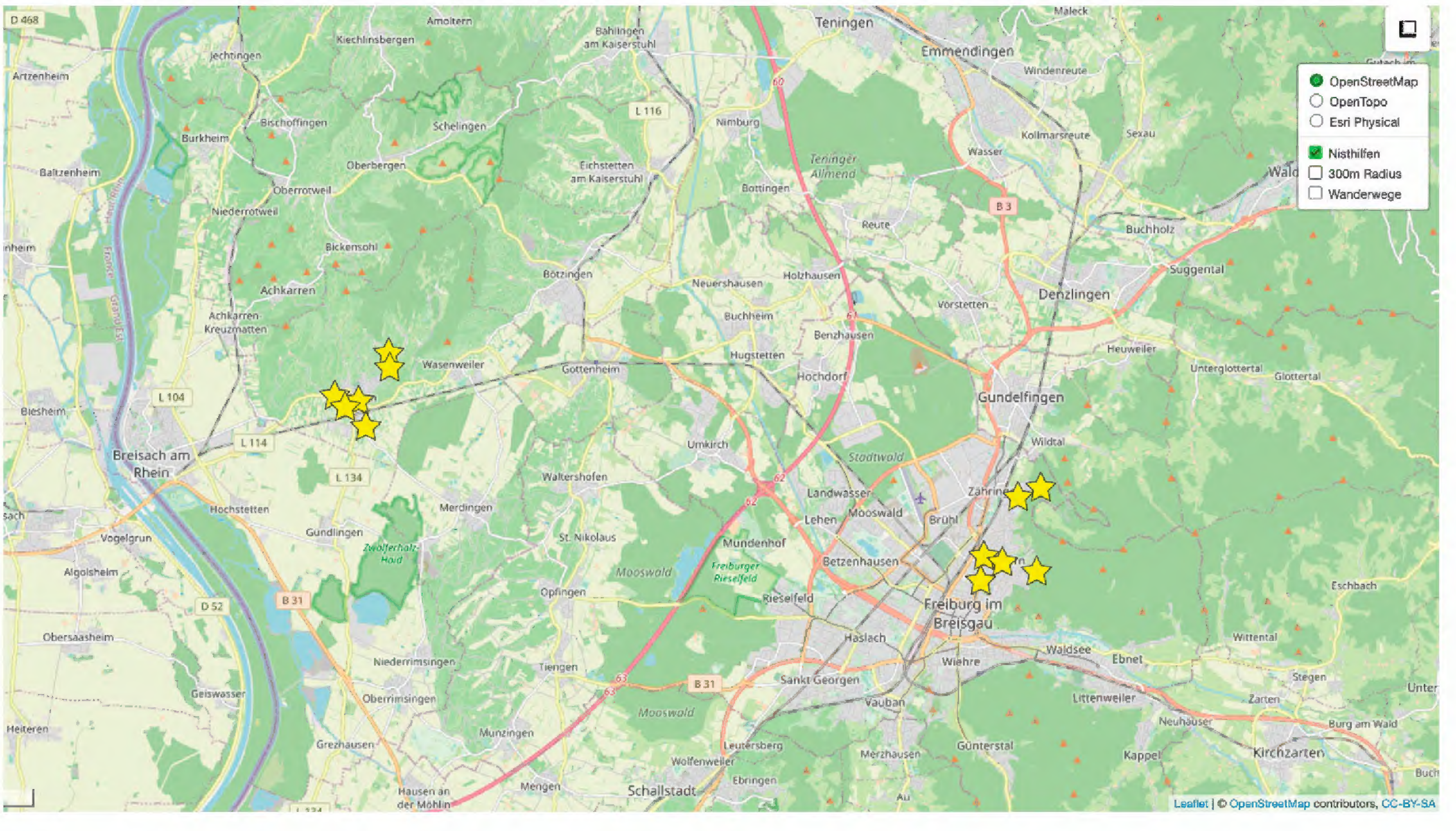

Figure 3. Freiburg city (right) and the vineyard Ihringen (left). Map from OpenStreetMap.

nesting aid for insects. Overview maps showing the locations of the layer nests are in the Suppl. materials 1, 2. The timing of the installation of the layer nests was matched with the flight period of *I. mexicana*, obtained from observations of adult *I. mexicana* on www.iNaturalist.org. The peak of observations covers mid-July to early September. Layer nests were deployed on 25th July 2022 and monitored until 30s August 2022.

Data analysis

For statistical analysis, all data were aggregated per site and analysis carried out in R version 4.3.2 "Eye Holes" (R Core Team 2025). A generalised linear model (glm) with a Poisson distribution was used to test if the number of prey individuals was dependent on the cavity diameter, and a linear model for testing if the number of *I. mexicana* eggs increased with the number of prey individuals in a cavity. To test for a relationship between prey size and cavity diameter, we tested the mean value of prey length per site in a linear model. The prey was measured with a slide gauge under the stereomicroscope (head without antennae to last tergite without cerci) and rounded up to whole mm.

Results

Isodontia mexicana nests were found at four out of 12 sites. *Isodontia mexicana* colonised our layer nests at only one out of four sites at which it was already present in pre-existing insect nesting aids, see Suppl. material 3.

All nests were found in Ihringen, the vineyard habitat. There were no findings in Freiburg, despite already existing occurrences and observed active nesting activities in the neighbouring nesting aids. We recorded a total of 407 Orthopterans, of which 297 were *Oecanthus pellucens* (238 females and 59 males) and 110 *Meconema meridionale* (57 females and 53 males). We found 55 completed brood cells with an egg inside. There were 352 grasshoppers in the 55 brood cells, one cell contained an average of 6.4 individuals of prey.

Preference for certain cavity diameters

Most of the 55 nests were found in the cavity diameters of 11 mm (Fig. 4). The 7 mm and 9 mm were chosen with similar frequency, the 5 mm cavities were not occupied at any site.

Relationship between prey length and cavity size

The body length of the prey individuals was approximately normally distributed, but *M. meridionale* is the smaller of the two species (Fig. 5). The mean body length of *M. meridionale* was 11.92 mm (SD = 0.95) and that of *O. pellucens* was 12.31 mm (SD = 1.02). Of the 407 prey individuals, body length determination was possible for 355 individuals. For the remaining individuals, measurement was not possible,

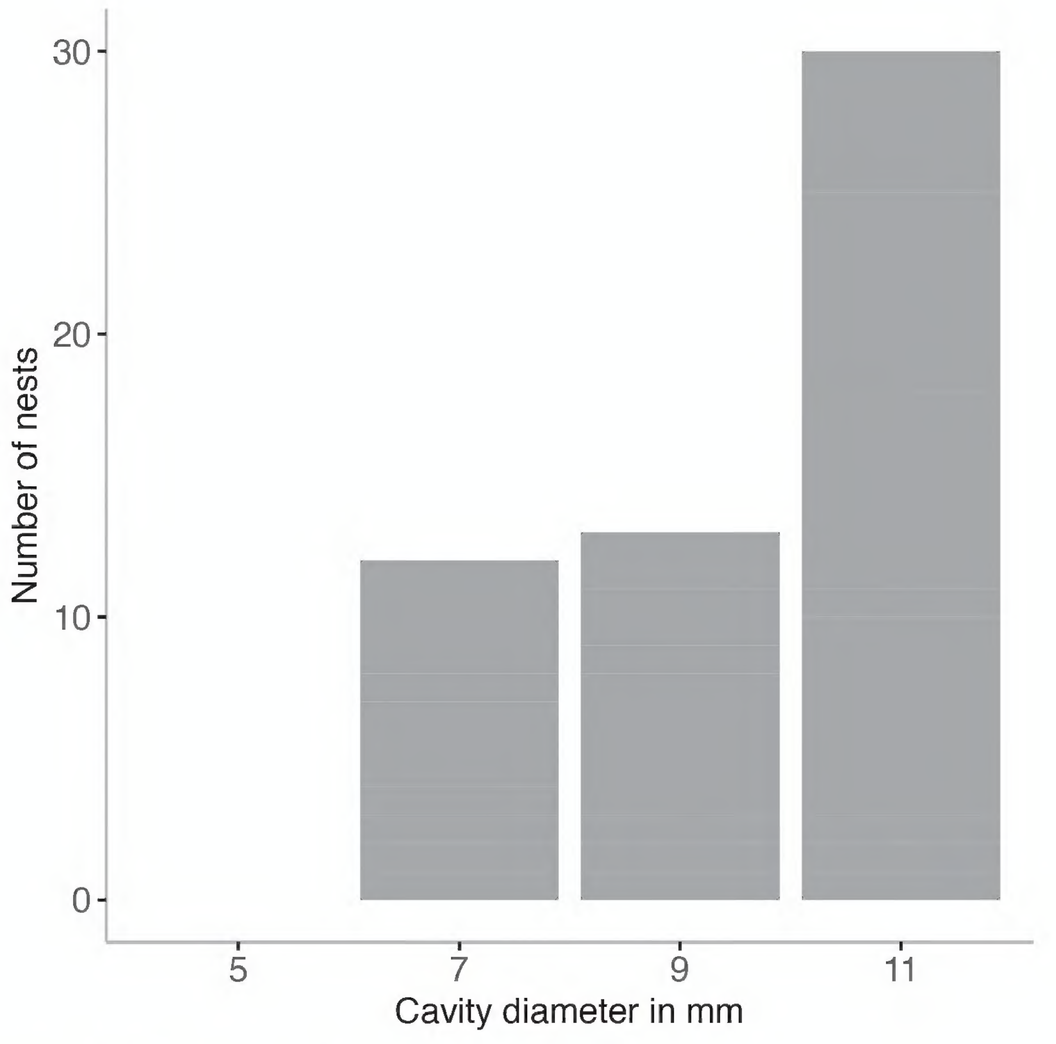

Figure 4. Number of *I. mexicana* nests per diameter.

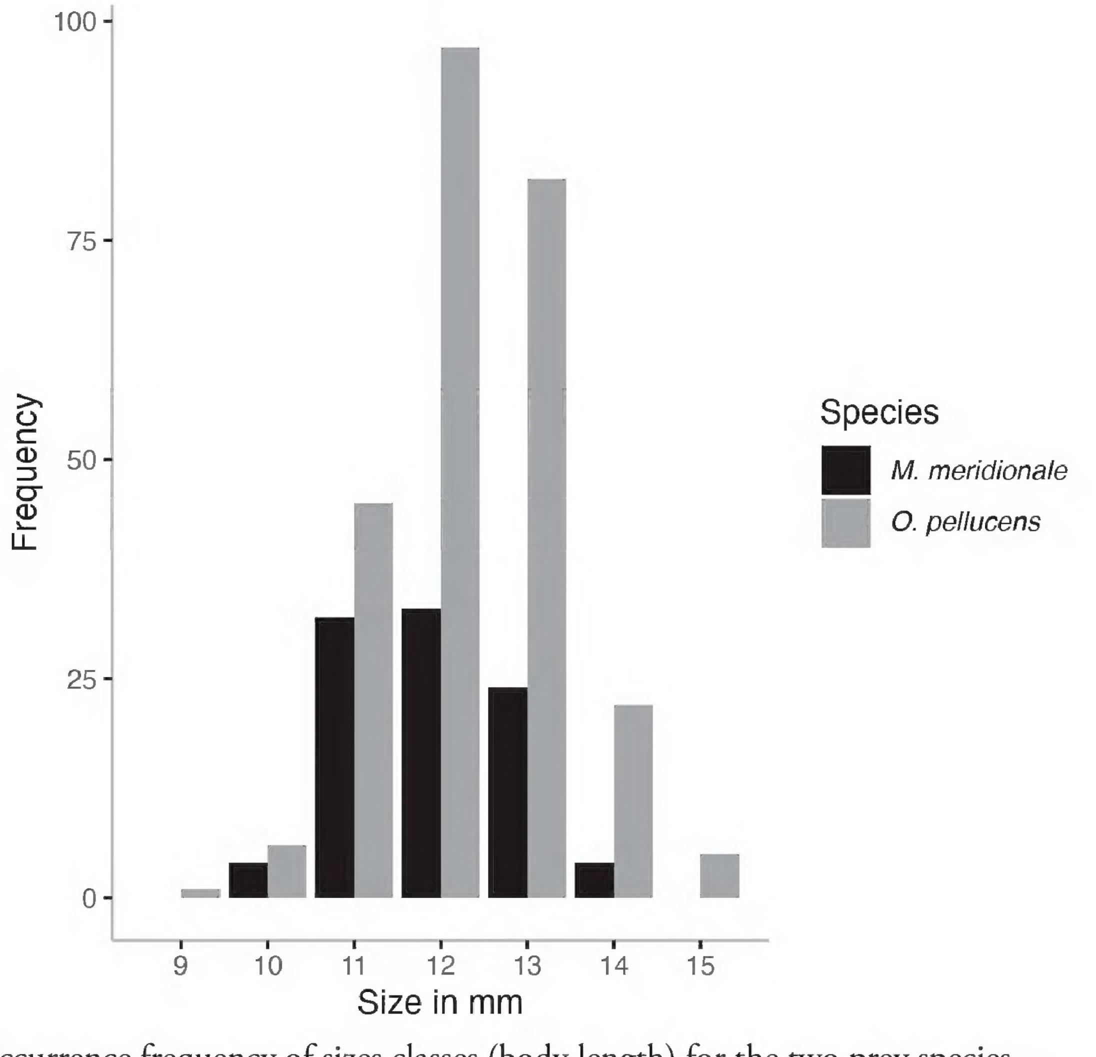

Figure 5. Occurrence frequency of sizes classes (body length) for the two prey species.

because the larvae of *I. mexicana* had already eaten the prey and only highly sclerotised body parts were present. Since leftovers included both wings and genitalia, we could still tell the species and sex of the prey. In total, we found no individual in cavities of 5 mm, 67 individuals (16.5%) in 7 mm, 81 individuals (19.9%) in 9 mm, and 259 individuals (63.6%) in 11 mm diameter. Mean body length of prey was not related to cavity diameter (Fig. 6). Number of prey individuals increased significantly with increasing cavity diameter (estimate = 0.372 ± 0.038 SE, $z = 9.817$, $p < 0.001$, Fig. 7).

The number of *I. mexicana* eggs per cavity increases significantly with the number of prey individuals per cavity (estimate = 0.0916 ± SE 0.009, $z = 9.852$, $p < 0.001$, Fig. 8).

Preference for lower layers

As no evidence of nesting site preferences within nest boxes was found in any literature so far, it was unexpected that *Isodontia mexicana* colonises the lower layer of the layer nest particularly frequently, shown as a bar chart in Fig. 9.

Fig. 10 shows the recorded prey per plate. The diagrams not only show a preference for the lower layer, but also that some prey was placed in the upper layer (layer 1), but no eggs, as shown in Fig. 9.

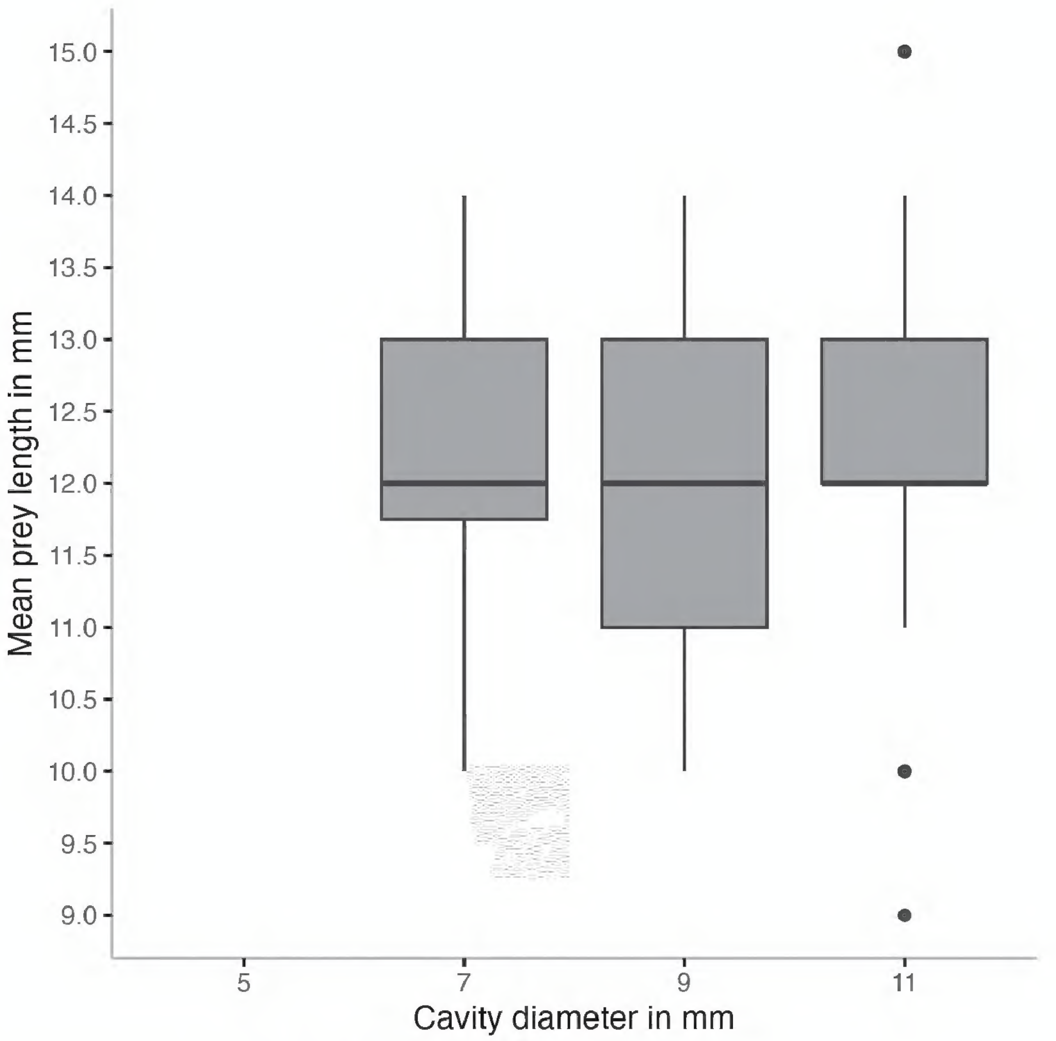

Figure 6. Mean prey length per cavity diameter.

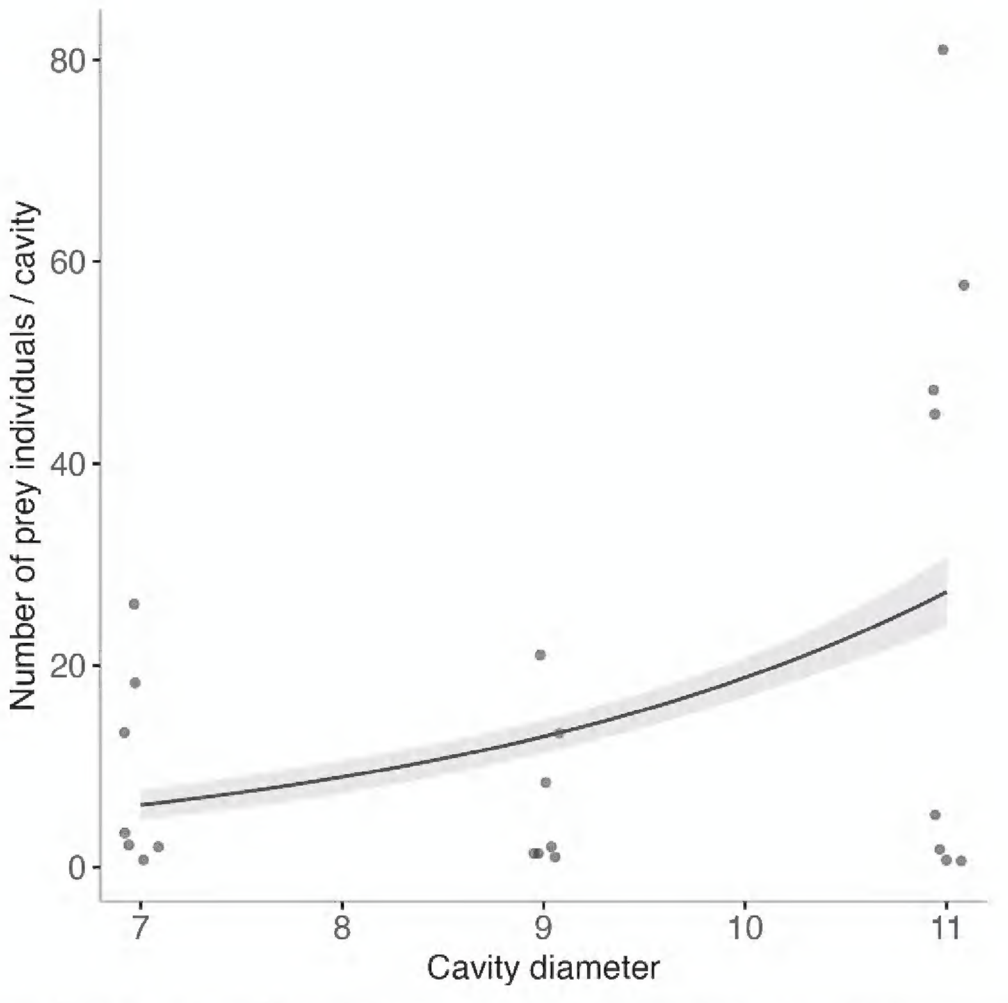

Figure 7. The number of prey individuals increases with increasing cavity diameter, model prediction line (solid line) ± SE (grey shaded area) and data points (dots with a slight x-axis jitter).

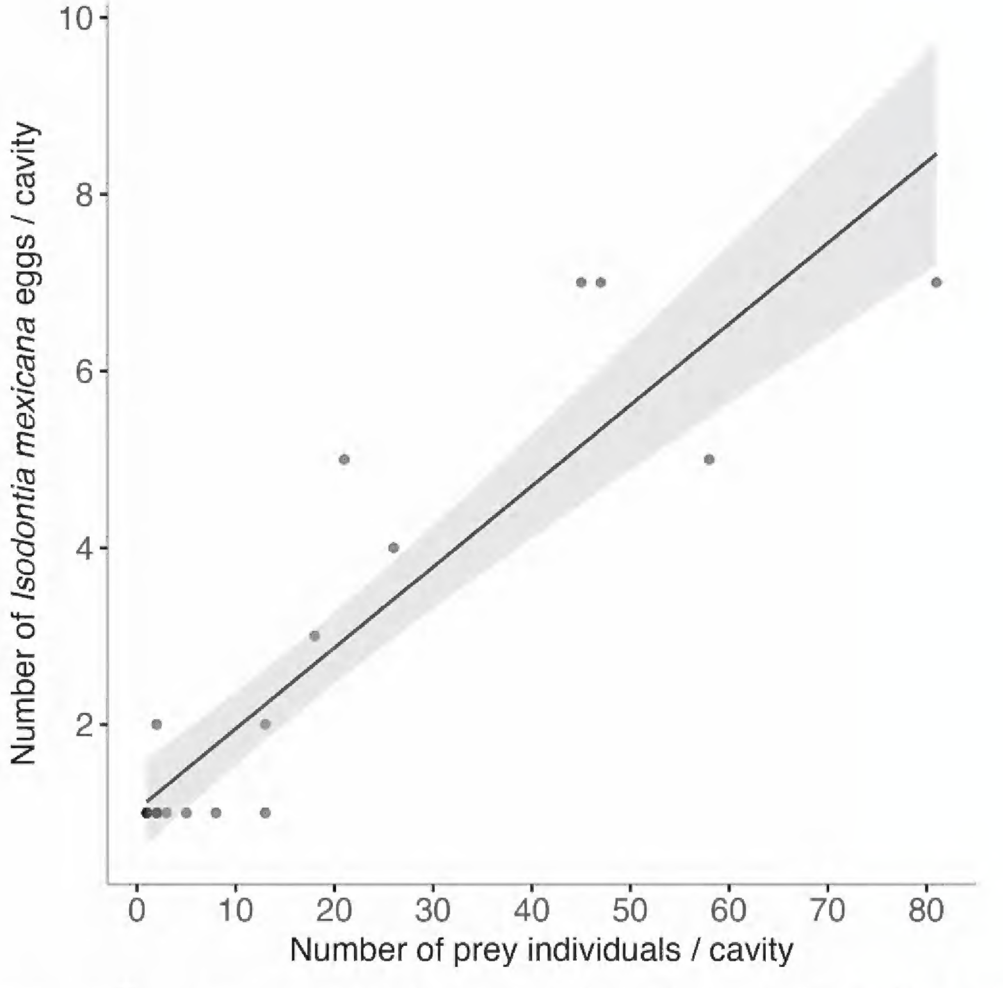

Figure 8. The number of eggs increases with the number of prey individuals, model prediction line (solid line) ± SE (grey shaded area) and data points (dots with a slight x-axis jitter).

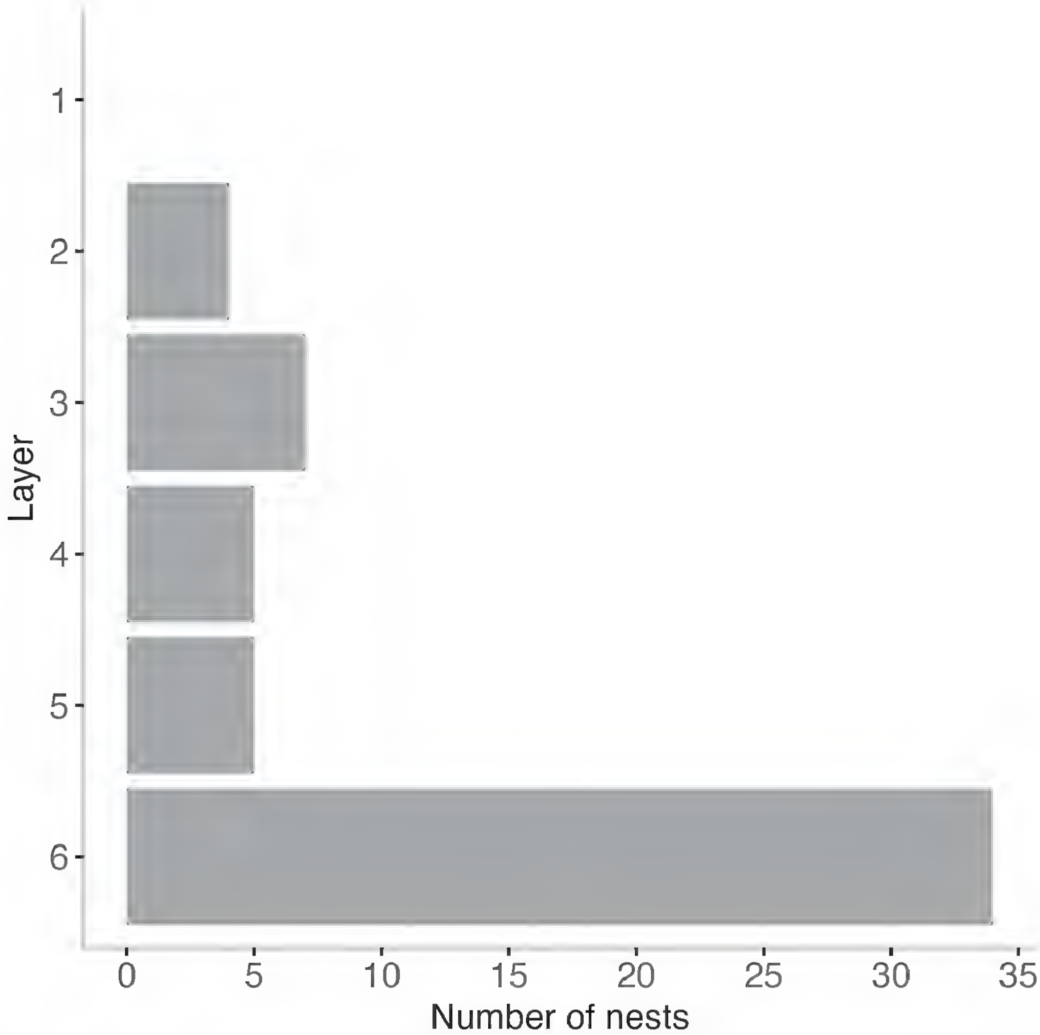

Figure 9. The number of nests per layer. Layer 1 is the top layer, layer 6 is the bottom layer.

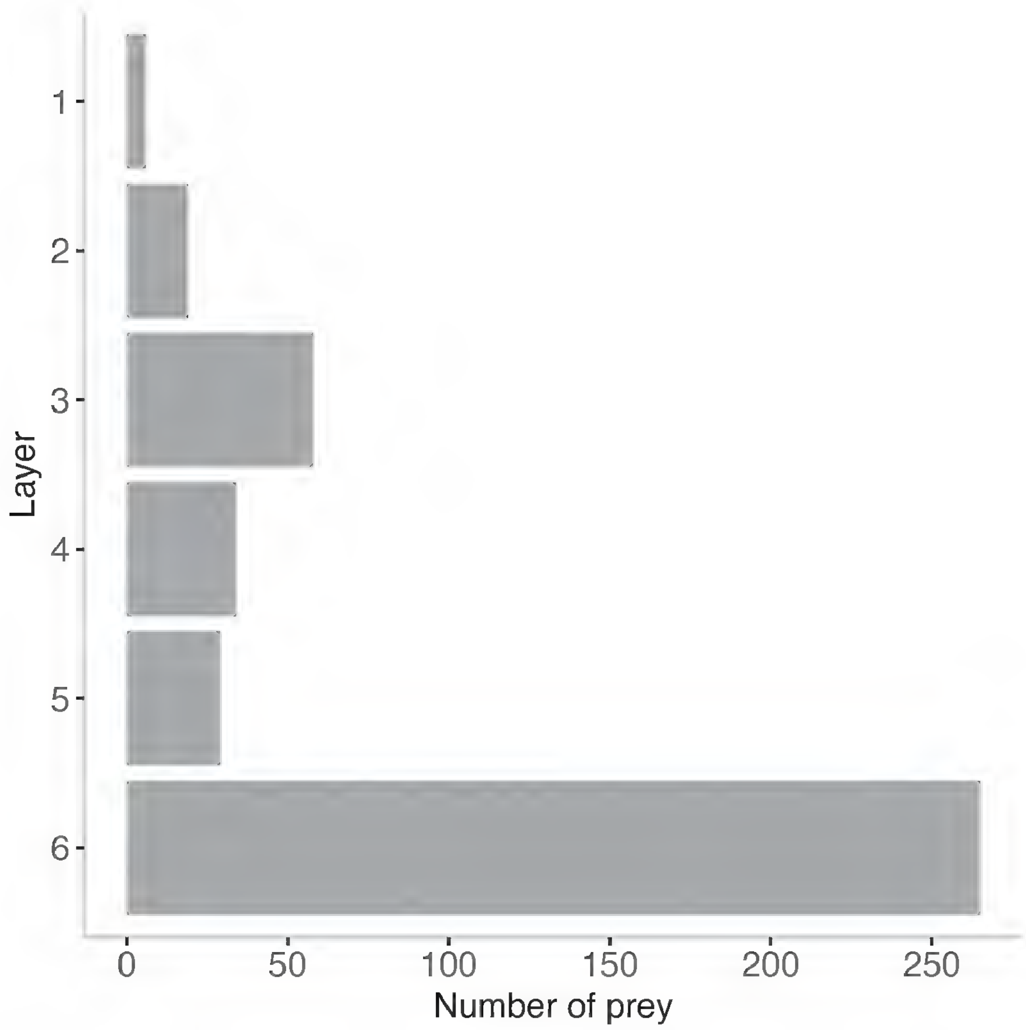

Figure 10. Number of prey individuals per layer. Layer 1 is the top layer, layer 6 is the bottom layer.

Discussion

In south-west Germany, *Isodontia mexicana* preferred large cavity diameters of 11 mm and used both *Oecanthus pellucens* and the more mediterranean distributed *Meconema meridionale* as prey for larval provision. Prey body length was not related to cavity diameter. Therefore, no obvious nest site competition with native bees and wasps is expected but further research on the natural history of this wasp and its effect on local Ensifera populations is needed.

Preference and competition with other cavity-colonising insects

When *Isodontia mexicana* has various cavities at its disposal, it prefers larger cavity diameters such as the 11 mm offered in this study. This result differs from the North American literature, which reports a preference for 6 to 7 mm (Medler 1965; O'Neill and O'Neill 2003) and the German literature, which reports 8 to 10 mm (Schirmel et al. 2020). Moreover, the 7 and 9 mm cavities were partly occupied in this study even when some 11 mm cavities were still unoccupied. Within smaller diameters, a competitive situation may arise with native cavity-nesting Hymenoptera. For example, *Osmia cornuta*, *O. bicornis* and *O. adunca* use the 7 mm to the 9 mm cavities (Westrich 2019). Many commercial nesting aids offer mainly very large cavity diameters, which are rarely used by native bees. For *I. mexicana*, this offers a resource that is almost unrivalled; only *Megachile sculpturalis*, another alien bee, which can itself be a competitor to native bee species, prefers large nest tubes and even robs out the nests of *I. mexicana* in order to use the vacated nesting space itself (Fornoff et al. 2024).

The late onset of breeding by *I. mexicana*, which is after the season of most bees, additionally weakens the direct competition, because the native bees have already occupied their nesting tubes by this time. However, they may lack nesting resources in the following spring when pupae of *I. mexicana* are still in the brood tubes occupying potential nesting opportunities. Further native bee species for example, *Anthidium manicatum* and *Megachile ericetorum*, that require larger cavities use nesting aid like structures, such as layer nests or reed trap nests, only occasionally (Westrich 2019; Lindermann et al. 2023). The species may use other structures, which may need consideration in terms of competition studies in the future. Our findings on nesting aids, such as layer nest, supports generally low competitive risk and highlights the importance of increasingly offering smaller and medium cavity diameters in artificial nesting boxes in order to specifically promote native bees (cf. MacIvor and Packer 2015; Geslin et al. 2020).

No correlation between prey length and cavity size

It could be expected that cavity diameter size limits the size of the prey individuals. However, our results show that prey size is not related to cavity diameter. This is likely explained by cavity diameters always exceeding the body diameters of prey items in our

study. Occupation of smaller diameters or use of larger prey items might have shown selective effects. However, we found grass-sealed cavities that contained only 1 to 2 orthopterans but no egg. Further investigations could identify if these are mock nests to distract predators and parasites from egg-bearing nests and whether these nests are more frequently created in small or otherwise less preferred cavities, such as upper layers in our layer nests. It would also be important to investigate whether there could be competition with other Specidae or other wasps.

Habitat differences

At Ihringen at the Kaiserstuhl, breeding activity of *Isodontia mexicana* was detected in four out of six trap nests. In Freiburg, none of the trap nests were occupied, although existing nests of *I. mexicana* were found at 2 of the 6 sites. It is possible that *I. mexicana* is already more established in Ihringen because the more rural structure offers it more diversity and supply of prey and nesting sites. Previous studies have shown that *I. mexicana* prefers such sites (Schirmel et al. 2020). In the Freiburg Botanical Garden, an actively nesting *I. mexicana* was observed during the field phase, possibly this female had chosen her breeding tubes beforehand and the layer nest was installed too late.

Differences in prey species

In the literature, there has not yet been a survey on the sex ratios of *Oecanthus pellucens*. In this study, the proportion of preyed females in *Meconema meridionale* was 52%, while females in *O. pellucens* accounted for 80%. For *M. meridionale*, this result is in line with the results of Schirmel et al. (2020). For *O. pellucens*, comparable sex ratios have been documented in North America, where females of *Oecanthus* sp. account for 81% of prey (O'Neill and O'Neill 2009). It is possible that female individuals of *Oecanthus* sp. are more common. To the best of our knowledge, no information on this is available in the literature. Another possibility is that females are easier prey for *I. mexicana* and are therefore introduced in greater numbers. It is also possible that *Oecanthus* females have a higher life expectancy and are therefore over-represented in late summer or that females are the preferred prey as they may contain more protein. With further investigations in these aspects, the effects of *I. mexicana* on prey populations could be better quantified.

Further nesting preference: the lower area of the nest

Unexpectedly *Isodontia mexicana* colonised the lower layers of the layer nest particularly frequently, depositing more prey items. In contrast upper layers were less frequently occupied and despite presence of prey items brood cells did not contain any eggs. This may indicate either that *I. mexicana* prefers cavities that are closer to the ground or that lower level layers have other benefits such as whether protec-

tion, which wasps might favour. We think that it is unlikely that wasps that carry prey items and nest materials for several (hundred) meters would discern between layers to save energy for nest provisioning by choosing an only a few centimeters (2–18 cm) less elevated nesting site. It is much more likely that top layers are more affected by temperature or humidity or their fluctuations which wasps perceive and potentially avoid. For example, if a wasp starts placing grasshoppers in a cavity of the upper layers but recognises throughout the day that this layer gets heated up by solar radiation more than the developing offspring may resist, it might move nesting activities to lower layers during the course of the day. However, it remains open why nests in the upper layer were still closed with grass sticks and if this hints towards the creation of mock nests.

Invasiveness

Isodontia mexicana was often referred to as invasive (Ćetković et al. 2012; Can 2024; Gladcaia 2024). However, the definition of this term is ambiguous due to its divergent usage across different sources. In the field of entomology, the term 'invasive' is typically applied to insects that have been shown to establish themselves in a new environment, spreading rapidly (Hastings et al. 2004) and causing substantial ecological (Kenis et al. 2009; Fortuna et al. 2022), economic or social harm (Mack et al. 2000; Bertelsmeier et al. 2024) in that environment. This distinction is crucial in differentiating invasive insects from those that are merely new, neozoic, or spreading. The duration of presence in a new area is not sufficient for this assessment; information on long-term integration is also required. The present work is intended to help with this categorisation for *I. mexicana*. We found no evidence of competition, but rather successful integration. With regard to this aspect, a categorisation would be neozoic rather than invasive.

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Supplementary material 1

Location of layer nests in Freiburg city

Authors: Sarah von Adelmannsfelden, Felix Fornoff

Data type: png

Explanation note: The locations of the layer nests within Freiburg city with theor radius of 300 meters.

Link: https://doi.org/10.3897/jhr.98.148947.suppl1

Supplementary material 2

Locations of layer nests in Ihringen

Authors: Sarah von Adelmannsfelden, Felix Fornoff

Data type: png

Explanation note: The locations of the layer nests within the vineyard with their radius of 300 meters.

Link: https://doi.org/10.3897/jhr.98.148947.suppl2

Supplementary material 3

Further informations to nesting sites

Authors: Sarah von Adelmannsfelden, Felix Fornoff

Data type: docx

Explanation note: All the sites and locations with information if *I. mexicana* is already nesting.

Link: https://doi.org/10.3897/jhr.98.148947.suppl3